NOTE / NOTE

“Recalcitrant understory layers” revisited: arrested succession and the long life-spans of clonal mid-successional species

Truman P. Young and Emily Peffer

Abstract: In their recent review of arrested succession, Royo and Carson (A.A. Royo and W.P. Carson. 2006. Can. J. For. Res. 36: 1345–1362) demonstrate that “recalcitrant understory layers” are widespread and pervasive modifiers of ecosystems and disruptors of forest regeneration. They rightly point out that many plant species associated with arrested succession are characterized by rapid vegetative spread. Extending their review, we point out that most of such species are clonal or thicket-forming and suggest that an additional reason why these plants so effectively suppress succession for extended periods is their long life-spans.

Résumé : Dans leur revue de littérature récente au sujet de l’interruption du processus de succession, Royo et Carson (A.A. Royo et W.P. Carson. 2006. Rev. can. rech. for. 36 : 1345–1362) démontrent que les strates récalcitrantes du sous-bois sont des agents envahissants et largement répandus de modification des écosystèmes et de perturbation de la régénération forestière. Ils font remarquer avec raison que plusieurs espèces végétales associées à l’interruption du processus de succession sont caractérisées par une propagation végétative. Poussant plus loin leur revue du sujet, nous soulignons le fait que la plupart des espèces sont clonales ou qu’elles forment des fourrés et nous soumettons l’idée que leur longévité est une raison additionnelle qui explique pourquoi ces plantes interrompent si efficacement le processus de succession pendant de longues périodes.

[Traduit par la Rédaction]

Succession is one of the core concepts in ecology and one of the oldest and most widespread ecological observations. The idea that communities can often recover from disturbance is also a useful starting point in ecological restoration, which seeks to repair damaged ecosystems. One major exception to the typical successional trend is the occurrence of numerous cases of arrested succession (also called truncated succession), in which early- and mid-successional species dominate the community so fully that later successional species are suppressed, and succession apparently ceases or is delayed far beyond what is considered typical or desirable. These species are considered major impediments to natural regeneration and ecological restoration (Young et al. 2001), particularly in forest ecosystems (but see Brantley and Young 2007).

This form of arrested succession is the subject of a recent synthetic review (Royo and Carson 2006). The authors demonstrate that “recalcitrant understory layers” are widespread and pervasive modifiers of ecosystems and disruptors of forest regeneration. They rightly point out that many species associated with arrested succession are characterized by rapid vegetative spread and suggest two reasons why such species would create recalcitrant understories. First, rapid vegetative spread may help these species to quickly dominate the understory vegetation. Second, their vegetative capabilities may make them less susceptible to elimination by the herbivores (or fire) that co-contribute to the suppression of late-successional species. We would like to suggest that an additional reason why these clonal and thicket-forming species so effectively suppress succession for extended periods is the long life-spans of their genets.

There appears to be a rough match between the persistence of species during succession and the characteristic life-spans of their individuals (or genets), perhaps because individuals of many species can establish only during relatively small successional windows and can persist as adults only for their own life-spans. This suggests that many successional species last for only a single generation (see the inhibition model of Connell and Slatyer 1977). Indeed, a common definition of the result of (forest) succession is that the “climax consists of those plants that can reproduce successfully beneath their own shade and therefore maintain the community indefinitely under prevailing climatic conditions” (Kimmins 1997, pp. 403–404).

We propose here that many cases of arrested succession and alternative stable states may be anomalous cases of

Received 23 March 2009. Accepted 15 March 2010. Published on the NRC Research Press Web site at cjfr.nrc.ca on 14 May 2010.

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Table 1. Species reported to suppress forest regeneration, and their growth forms (adapted from Royo and Carson (2006), with a few typographic corrections and additional species and references).

Species	Family	Clonal or thicket-forming?	Reference(s)
Ferns			
Dennstaedtia punctilobula	Dennstaedtiaceae	Yes	See Royo and Carson 2006; Hill and Silander 2001
Pteridium aquilinum		Yes	See Royo and Carson 2006
Thelypteris noveboracensis	Thelypteridaceae	Yes	See Royo and Carson 2006
Blechnum spp.	Blechnaceae	Yes	See Royo and Carson 2006
Cyathea spp.	Cyatheaceae	??	See Royo and Carson 2006
Dicranopteris linearis	Gleicheniaceae	Yes	See Royo and Carson 2006; Ashton et al. 2001
Dicranopteris pectinata		Yes	See Royo and Carson 2006; Slocum et al. 2004, 2006
Gleichenia bifida		Yes	See Royo and Carson 2006
Gleichenia linearis		Yes	See Royo and Carson 2006
Bamboos			Tabanez and Viana 2000
Sinarundinaria gangiana	Poaceae	Yes	See Royo and Carson 2006
Chusquea spp.		Yes	See Royo and Carson 2006
Guadua sarcocarpa		Yes	See Royo and Carson 2006
Fargesia denudata		Yes	See Royo and Carson 2006
Sasa spp.		Yes	See Royo and Carson 2006
Yushania microphylla		Yes	See Royo and Carson 2006
Other grasses			
Andropogon scoparius	Poaceae	Yes	Niering and Goodwin 1974
Calamagrostis canadensis		Yes	See Royo and Carson 2006
Cortaderia spp.		Yes	See Royo and Carson 2006
Deschampsia flexuosa		Long-lived tussock	See Royo and Carson 2006
Pennisetum purpureum		Yes	Zanne and Chapman 2001
Setaria sphacelata		Long-lived tussock	Sarmiento 1997
Cymbopogon nardus		Yes	Zanne and Chapman 2001
Panicum maximum		Yes	Kent et al. 2000
Palms			
Asterogyne martiana	Arecaceae	Yes	see Royo and Carson 2006; Cooley et al. 2004
Geonoma cuneata		Yes	See Royo and Carson 2006
Oenocarpus mapora		Yes	See Royo and Carson 2006
Clonal herbaceous plants			
Asplundia uncinata	Cyclanthaceae	Yes	See Royo and Carson 2006; Cooley et al. 2004
Aechmea magdalenae	Bromeliaceae	Yes	See Royo and Carson 2006; Cooley et al. 2004
Clonal ericaceous shrubs			
Calluna vulgaris	Ericaceae	Yes	See Royo and Carson 2006
Kalmia angustifolia		Yes	See Royo and Carson 2006; Niering and Goodwin 1974
Kalmia latifolia		Yes	See Royo and Carson 2006; Niering and Goodwin 1974
Rhododendron maximum		Yes	See Royo and Carson 2006; Niering and Goodwin 1974
Gaylussacia baccata		Yes	See Royo and Carson 2006; Niering and Goodwin 1974
Gaultheria shallon		Yes	See Royo and Carson 2006
Vaccinium myrtillus		Yes	See Royo and Carson 2006
Vaccinium vacillans		Yes	Niering and Goodwin 1974
Vaccinium corymbosum		Yes	Niering and Goodwin 1974
Empetrum hermaphroditum		Yes	See Royo and Carson 2006

Table 1 (*concluded*).

Species	Family	Clonal or thicket-forming?	Reference(s)
Lianas and vines			
Various species	Various	Long-lived, sprawling in gaps	See Royo and Carson 2006; Schnitzer et al. 2000; Tabanez and Viana 2000; Ashton et al. 2001
Lonicera japonica	Caprifoliaceae	Yes	Niering and Goodwin 1974
Clonal and thicket-forming shrubs			
Juniperus communis	Cupressaceae	Yes	Niering and Goodwin 1974
Acanthus pubescens	Acanthaceae	Yes	Chapman et al. 1999; Paul et al. 2004
Isoglossa woodii	Acanthaceae	Yes	Griffiths et al. 2007
Quercus ilicifolia	Fabaceae	Yes	Niering and Goodwin 1974
Rubus spp.	Rosaceae	Yes	See Royo and Carson 2006
Spirea latifolia		Yes	Niering and Goodwin 1974
Baccharis trinervis	Asteraceae	Yes	Zahawi and Augspurger 1999
Ceanothus velutinus	Rhamnaceae	Yes	Niering and Goodwin 1974
Rhus glabra	Anacardiaceae	Yes	See Royo and Carson 2006
Smilax rotundifolia	Smilicaceae	Yes	Niering and Goodwin 1974
Hamamelis virginiana	Hamamelidaceae	Yes	Niering and Goodwin 1974
Viburnum lentago	Caprifoliaceae	Yes	Niering and Goodwin 1974
Viburnum recognitum		Yes	Niering and Goodwin 1974
Corylus cornuta	Betulaceae	Yes	See Royo and Carson 2006, Niering and Goodwin 1974
Alnus rugosa		Yes	Niering and Goodwin 1974
Cornus spp. (including *C. racemosa*)	Cornaceae	Yes	See Royo and Carson 2006; Niering and Goodwin 1974
Acer spicatum	Aceraceae	Yes	See Royo and Carson 2006 and www.rook.org/earl/bwca/nature/shrubs/acerspic.html
Comptonia peregrina	Myricaceae	Yes	Niering and Goodwin 1974
Myrica cerifera		Yes	Crawford and Young 1998
Nonclonal(?) species			
Pseudowintera colorata	Winteraceae	No?	See Royo and Carson 2006

Note: For original references see Royo and Carson (2006).

early- and mid-successional species (especially clonal spp.) whose individuals have uncharacteristically long life-spans. Clonal and suckering (coppicing) growth forms can extend plant life-span of genets far beyond the life-span of individual ramets, even indefinitely (Watkinson and White 1986; Silvertown et al. 2001; Tanner 2001). If so, succession in these situations may be moving along at the same relative (generational) schedule as in other forests but delayed (or arrested) in real time because of the extraordinary life-spans of these clonal mid-successional plants.

We reviewed the species in Royo and Carson's (2006) table 1, and our own literature search found an additional 17 papers and 21 species (Table 1). In particular, Niering and Goodwin (1974) is a rich source of examples where clonal species appear to arrest succession and create alternative community states that are stable for at least several decades. This review showed that virtually all of the >50 documented suppressing species are clonal or form suckering thickets: clonal ferns (≥9 spp.), clonal bamboos (≥6 spp.), other clonal and long-lived clump grasses (≥8 spp.), clonal palms (3 spp.), clonal herbs (2 spp.), clonal ericaceous shrubs (10 spp.), other clonal or thicket-forming shrubs (≥19 spp.), and lianas (≥5 spp.). For a list of additional candidate species in managed rights-of-way, most of them clonal, see Shatford et al. (2003).

Another contributor to the persistence of these species may be that clonal integration can produce clones that subsidize particularly high stem and foliage densities and produce low light levels (see Griffiths et al. 2007) that resist invasion by other species through space and resource preemption (Herben and Hara 1997; Pyšek 1997). There may be a trade-off between the ability of clonal organisms to invade space and resist invasion. Runner ("guerilla") species produce long rhizomes and excel at rapidly invading new territory, whereas clumper ("phalanx") species form dense thickets and may be superior at holding onto space (Gough et al. 2002).

We suggest that it is the life-spans of these clonal plants, as much as or even more than the speed of their vegetative growth, that maintains arrested successional states. In fact, Nesmith et al. (2006) suggest that the more slowly expanding clones of *Symphoricarpos hesperius* G.N. Jones are more effective at producing dense, suppressing thickets than the more rapidly expanding clones of *Rubus ursinus* Cham. & Schltdl. (see also Gough et al. 2002). In addition, many early and mid-successional stages are characterized by dense vegetation, but it is only when this vegetation stage is composed of clonal and(or) thicket-forming species that it appears to be strongly suppressive of forest succession for long periods of time. It is perhaps not surprising that many of the most pernicious exotic invaders of forest ecosystems are also clonal (e.g., in California, Himalayan blackberry, tree of heaven, cape ivy, English ivy, black locust, Brazilian pepper tree, tamarix; K. Holmes, personal communication, 2008; see also Reichard and Hamilton 1997).

This does beg the question of why these species sometimes come to dominate successional series in the first place and sometimes do not. We agree with Royo and Carson that there appears to be a synergism between vegetative growth and large mammal herbivory (and other disturbances, such as fire). For example, *Acanthus pubescens* Delile var. *pseudopubescens* Cufod. suppresses forest succession in Uganda (Chapman et al. 1999; Paul et al. 2004), but only in the presence of elephants that suppressed other woody species more than *Acanthus* (Lawes and Chapman 2006; see also *Alnus rugosa* (L.) Moench ssp. rugosa (Du Roi) R.T. Clausen in Niering and Goodwin 1974).

If the long life-span and competitive suppression of these clonal species explains their dominance, one might ask what eventually brings this dominance to an end and allows forest to regenerate. Several factors may contribute. Firstly, although these clonal species suppress many tree species, other tree species may still manage to grow though and overtop them (George and Bazzaz 1999; Caccia et al. 2009). Secondly, herbivores may knock back clonal species and allow tree regeneration (Darabant et al. 2007). And lastly, even self-renewing and long-lived clonal individuals may reach a senescent stage. In particular, some of these clonal species are semelparous, flowering and dying synchronously at long intervals, again giving trees the opportunity to regenerate (Taylor et al. 1995; Griffiths et al. 2007; Holz and Veblen 2006; Giordano et al. 2009).

The life-span hypothesis raises (testable) questions. Firstly, how common is it in forest succession for species to last only a single generation? Secondly, what is the life-span of the clonal plants that dominate recalcitrant understory layers, and does the delayed succession proceed after they have reached senescence? It might be particularly useful to examine species that vary in rate of clonal spread, density of ramets, and life-span, and to compare the relative contributions of these factors with the creation and maintenance of recalcitrant understory layers (W. Carson, University of Pittsburgh, personal communication, 2007; see Nesmith et al. 2006).

Acknowledgements

This note benefited from feedback provided by Walter Carson, Alex Royo, Lauren McGeoch, Colin Chapman, Katherine Holmes, Don Stratton, Zak Zahawi, and anonymous reviewers.

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